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ECOLOGICAL PROBLEMS OF THE HUMUS LAYER IN THE FOREST

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ECOLOGICAL PROBLEMS OF THE HUMUS LAYER IN THE FOREST

L. G. ROMELL

THE HUMUS LAYER IN FOREST ECOLOGY

Forest-soil study is a separate branch of science, distinct from agricultural soil technology simply because of the fundamental difference between an extensive form of land use, such as forestry, and an intensive form, such as agriculture (Romell, 1930). Agriculture, even in its extensive forms, is based on some sort of technic creating and maintaining distinctly artificial conditions. Forestry must depend upon natural or slightly modified ecological factors and equilibria.

In particular, the important rôle of fertilizing and soil-working is, in forestry practice, assigned to man only in exceptional cases, as a temporary or an emergency measure. This fact gives special importance in forest-soils work to the study of the humus layer, that is, the horizon of humus formation, the seat of the briskest activity of the soil life. The biological processes concentrated to the humus layer have to supply, among other things, the nitrogen food required by the forest trees for a satisfactory production.[2]

Humus was earlier regarded as the very essence of soil fertility. Recently the tendency is rather the opposite, the humus having been labeled as a nuisance or a necessary evil (Süchting, 1929a). Instead, a rapid and complete decomposition is taken as the ideal. Both the old and the extreme recent view are based on false generalizations, expressed in the very meaning of the word "humus" during different times. To the early authors, true humus mostly was humus incorporated in the soil. Today, the term is often used much as a synonym of "Auflagehumus" (cover humus, unincorporated humus). One or the other kind of humus predominates in different types of humus layer. The real index of fertility level is less the amount of humus, of whatever kind, than it is the type of humus formation.

The important differences in the type of humus formation in the forest were early dimly conceived by nature-observing foresters. Hundeshagen (1830), although hesitating about taking a view so little scientific, distinguished two "main conditions" with respect to "the origin and effect of the humus." He felt that this distinction would be particularly important, "at least for practical application," in the same measure as "the theory about these things is developed." This remarkable forecast, which seems completely forgotten in the later literature, came true through the keen nature observer, P. E. Müller (1887), who rediscovered Hundeshagen's two main types of humus layer and was the first to apply consistently a point of view of soil biology to the problem. As testified by Hauch (1919), this work came as a revelation to Danish foresters, tapping around in the

[1]The present paper may be taken as a second and concluding part of an earlier article (Romell, 1932), but it has been written as an independent paper and on a slightly different plan.

[2]The nitrogen of the litter is largely unavailable until it has become "mineralized." Thus the statement made holds even where the nitrogen in rain and snow covers that fraction of the annual nitrogen consumption which is stored up in wood, as is still held by some authors (Leiningen-Westerburg, 1931) to be normally the case.

dark particularly with respect to the difficulties with beech regeneration. The work also laid the lasting ground for the biological forest-soil science.[3]

P. E. Müller's two main types of humus layer, mull and mor, are now accepted internationally, with the same designations (International Union of Forest Research Organizations, 1933). As explained elsewhere (Romell and Heiberg, 1931), they are characterized by structural and other differences directly observable in nature.[4] So are the subtypes, which are needed for further distinction particularly in this country. This does not mean that the types are unscientific makeshifts and are separated according to "the most superficial characteristics," as judged by Süchting (1929 b). The differences in layering, structure, and so forth, testify of important differences in soil life and in the course of decomposition, as should be clear after Müller's classical studies. Mull and mor have been found useful and natural types also in this country. For the purposes of the present paper, the broad division into these two main types, or type groups, is mostly sufficient. Only a few of the several specific types or subtypes (Romell and Heiberg, 1931) are occasionally mentioned.

Mull is an ecologically richer type than mor. Its more luxuriant vegetation is richer in species, and includes nitrate plants which are absent on undisturbed typical mor. With the more requiring tree species, mull is silvically favorable or is even a condition necessary for success. Most of the more valuable northeast-American broad-leaved trees, such as white ash, hickories, tulip poplar, and basswood, are believed to be such mull species (Romell and Heiberg, 1931). With a number of conifers mull may be unfavorable, being too rich. Red spruce does not do well on mull in the Adirondacks, in competition with hardwoods (Heimburger, 1934). Even direct unfavorable effects may appear, such as poor form and heavy limbs in Scotch pine, and heart rot and apparently reproduction difficulties (Lindquist, 1932) in Norway spruce. Otherwise at least the latter species, like white pine (Romell and Heiberg, 1931) and several other conifers, can utilize the richer conditions offered by a mull for better production. Forest production is not necessarily higher on mull, however. At least some of the famous mixed pine and spruce stands at Jönåker in Sweden (Schotte, 1921), corresponding to Schwappach's site class I, grow on mor soil. A forest soil may also be too shallow for good forest production, owing to ground water or some other factor, and yet have a good mull type of humus layer. It is seen that the relation between type of humus layer and the silvical characteristics of a forest soil is complicated. Yet the relation is evident and has been found very important.

Varied are also the factors favoring the development of one or the other type of humus layer. Generally speaking, mor is predominant in the belt of coniferous forests on podsol soils extending through the colder parts of the Temperate Zone, with oases of mull in localities favored by lime in rock

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[3] That is, in the North. In Germany, P. E. Muller seems to be practically forgotten today, as can be seen in the numerous volumes of Blanck's *Handbuch der Bodenlehre* and elsewhere.

[4] In the paper quoted (Romell and Heiberg, 1931), and also later (Romell, 1932), mor was called "duff." The arguments against the term "mor" disappeared in consequence of a congress resolution (Internat. Union Forest Research Organ., 1933) implying that Hesselman's "mor" (for a subtype) is retracted. The writer heartily joins in the general acceptance of the term "mor" strictly in P. E. Muller's sense. He is unable, however, to accept Bornebusch's definitions of mull and mor. They do not clearly refer to types of humus layer, but, in Ramann's fashion to "humus." This sort of classification is open to the harsh criticism of Süchting (1929 b), whereas a classification of types of humus layer in Muller's spirit is not. Moreover, Bornebusch's definition of mull does not fit conditions in nature, at least not in the United States (Romell, 1935).

and in soil or by drainage conditions (slopes with high and yet not stagnating ground-water, even in regions very poor in lime). Mull is characteristic of the forests of mostly broad-leaved trees extending in a zone with a somewhat milder temperate climate, much independently of geology but with islands of mor on too dry, too wet, and geologically very poor sites. In regions with an intermediate climate, as in Denmark and in large parts of New York State, mull and mor may alternate very locally, following variations in drainage conditions, forest stand, exposure, and geology.

In many cases, as in the beech forests in Europe, the mull is correlated to a brown forest-soil profile. In other cases, as in oak forests both in Scandinavia and particularly in Russia, a combination of a mull type of humus layer with a podsol profile is extensively found (Müller, 1924; Tamm, 1930, a and b). In northeastern United States, the more pronounced forms of mull are usually combined with a brown forest-soil profile. Less pronounced mull forms and light forms of mor may be combined with interesting profile types intermediate between podsols and true brown forest soils, as very frequently in the Adirondack Mountains (Heimburger, 1934).

Under uniform climatic and edaphic conditions, the composition of the stand has often been seen to affect the type of humus layer (Müller, 1887; Hesselman, 1926; Plice, 1934). Forestry operations also may have a striking effect, even though not changing the mixture of species in the stand (Hesselman, 1917b; Møller, 1931). Such different measures as thinnings, covering with green slash, clear cutting, light burning, ripping of the mor cover or any other form of soil working, and liming, have shown a surprisingly similar effect in activating a mor, starting nitrification and frequently changing the humus layer also morphologically to approach or even to become a mull. The same activation effect can be seen as a result of the girdling practices recently in favor in this country. It may also set in under an undisturbed tree cover as a result of trenching, burning, and other disturbances (Toumey, 1928; Gast, 1930; Fivaz, 1931). On the other hand, lack of protection of the ground has long been known to easily start a degeneration of a good mull condition (Müller, 1891?, 1894). This may lead in bad cases to the formation of a bothersome mor.

The most striking type conversions from influences such as those mentioned have been observed in regions with intermediate climatic and other conditions, as in south Scandinavia and on the Harvard Forest in Massachusetts (Fisher, 1928). Yet mor activation occurs from regular forestry practices right in the heart of climatically predetermined mor regions, as in north Scandinavia. However, it takes more drastic measures to start the activation under severer conditions. Clear cutting may be efficient where thinnings are not. The last resource among the cheaper, more extensive measures is a light burning of the clear-cut areas. This is much used in northern Sweden to activate the more refractive forms of mor. All these type-conversion and mor-activation effects are of the greatest importance silviculturally. The Danish beech silviculture is one continuous fight for the maintenance of a good mull, which is essential not only for reproduction of beech but also for its good growth. In north-Scandinavian forestry, based on pine and spruce, a sufficient activation of the mor is essential for a successful regeneration (Hesselman, 1917 b). Examples could be quoted as well from other countries.

A curious fact, and one not satisfactorily explained, is that the same measure may affect a mor not only to a different degree, but also in opposite directions, under different conditions. A selective diameter cutting may be fairly good silviculture with the better forms of mor in central Scandinavia, but in the North it has produced a mor worse than the average. Clear cutting is universally good in north Sweden, although not always in itself sufficiently activating; but it is feared by foresters in the Black Forest in southwestern Germany, as aggravating instead of improving a mor condition.

Even very heavy and pronounced northeast-American forms of mor (belonging to or approaching the greasy type) react with an ease surprising to a European observer. They seem to be activated by the slightest disturbances. The reason for their greater reactivity has not been explained.

THE ECOLOGICAL ENVIRONMENT IN MULL AND IN MOR

Variations in the degree of intermixing between humus and mineral soil, in aeration, in acidity and related characteristics, and in nitrogen mobilization, have been proposed as ecologically significant environmental differences between mull and mor.

The extensive mixing of humus with mineral soil has been regarded, both by older and by more recent authors, as a chief factor favorable both to higher plants growing on a mull soil and to the bacterial soil life. It cannot, however, in itself be regarded as constituting a group difference between mull and mor. It is characteristic of the crumb mull and related forms, rather than of the mull group. Moreover, there are exceedingly poor mor soils, for example those of the Danish heaths, which may contain just as much, if not more, humus intimately mixed with mineral soil as do rich mull soils. The difference between mull and mor lies rather in the way in which a mixture of humus with mineral soil is formed.

P. E. Müller made an exceptional mistake in assuming the aeration to be generally poor in and under a mor cover. He used this assumption in explaining the properties of the mor and its effect on the underlying mineral soil. This idea seems still to be held by some authors, although it has been conclusively disproved (Romell, 1922). Apart from these results, the notorious abundance of fungi in mor speaks distinctly against the idea of poor aeration, since very few anaerobic fungi are known.

If any kind of mor is characterized by poor aeration, it should be the pronounced greasy types, containing few living hyphae in their heavy and compact H-layer (highly humified horizon). In order to test this point, the oxidation-reduction potential of the best type of mull (crumb mull from Enfield, New York) was compared with that of the heaviest and most typical hemlock mor which could be procured in the vicinity (from Ellis Hollow, near Ithaca, New York). Both were used fresh.

The equilibrium to be measured takes a long time to establish itself (Wurmser and Geloso, 1928), and during that time air must be carefully excluded. Thus, highly unnatural conditions are created which may start processes foreign to the soil in its natural state. As a compromise between different considerations, the temperature was maintained at 60° C. to exclude most of the biological activity and shorten the time needed without too greatly hastening unnatural, purely chemical, changes of the mate-

rial. A 3-per-cent dextrose solution was included in the test, for comparison. All three samples were adjusted to pH 6.6, phosphate buffers being used. Potentials were measured between either of two 15-cm-long fine platinum wires in each flask with soil suspension or dextrose solution, and another platinum wire in phosphate buffer of pH 6.6 kept at 60° C. and saturated with quinhydrone before measuring. Phosphate buffer was used as a bridge between the half-cells. The potentials were approximately constant after four to five days at 60° C. At the end of the experiment, quinhydrone was added to the flasks and another reading was taken as a check on the pH. The figures recorded are as follows:

	Mor	Mull	Dextrose
Potential (volts)	−0.28	−0.51 to −0.52	−0.31 to −0.32
Potential with quinhydrone (volts)	+0.025	+0.025	+0.020

Thus the mull suspension was found to be rather strongly reducing, but the mor suspension was less reducing than dextrose. When the flasks were opened, the mull suspension smelled strongly like horse manure just excreted, while the mor suspension had the normal smell of boiled mor. The setting-in of anaerobic processes in water-logged mull can be demonstrated by simpler means at ordinary temperatures.

The result shows that the mor did not contain any strongly reducing substances indicating poor aeration. The writer is of the opinion that a good crumb mull, rather than any form of mor occurring on normally drained land, is likely to contain more or less anaerobic centers during wet periods (in the interior of its rather large crumbs). This may be of importance, for instance by creating conditions for nitrogen fixation by Clostridium. At any rate, there are no indications of a group difference in the other direction, as has been supposed.

A difference in acidity between mull and mor was noticed long before the modern technic was developed to measure it (Müller, 1887). Generally speaking, the acidity increases rather regularly from the best mull to the worst very acid mor, as is shown on American material by a rather extensive set of data (Romell and Heiberg, 1931; Heimburger, 1934). There is considerable variation, however, in individual samples, so much so that hard and fast boundaries as to acidity can hardly be drawn even between extreme types.

It was early noticed (Emeis, 1875; Müller, 1887) that mull and mor give extracts of different colors, either with distilled water or with weak ammonia (Schütze's test). The less intense humus color of mull extracts would indicate a greater base saturation of the humus colloids in the mull, according to modern ideas on the subject. This may not be the whole explanation, since the "humus colloids" in mull and those in mor may be entirely different (Plate I). Yet the simple extraction test would be worthy of a renewed investigation. Recently attempts have been made, by ion-exchange methods, to determine base saturation or unsaturation, either as such or as exchange acidity. For various reasons, however, the data thus far appear to be insufficient for judging whether differences of this order are more consistently characteristic of different types of humus layer than are the actual acidities. The considerable work done in the writer's laboratory on this problem did not advance further than to a critical study of methods. Promise was given by the barium-acetate

method, even with difficult samples from greasy types; whereas the ammonium-acetate method broke down completely on samples of this kind.

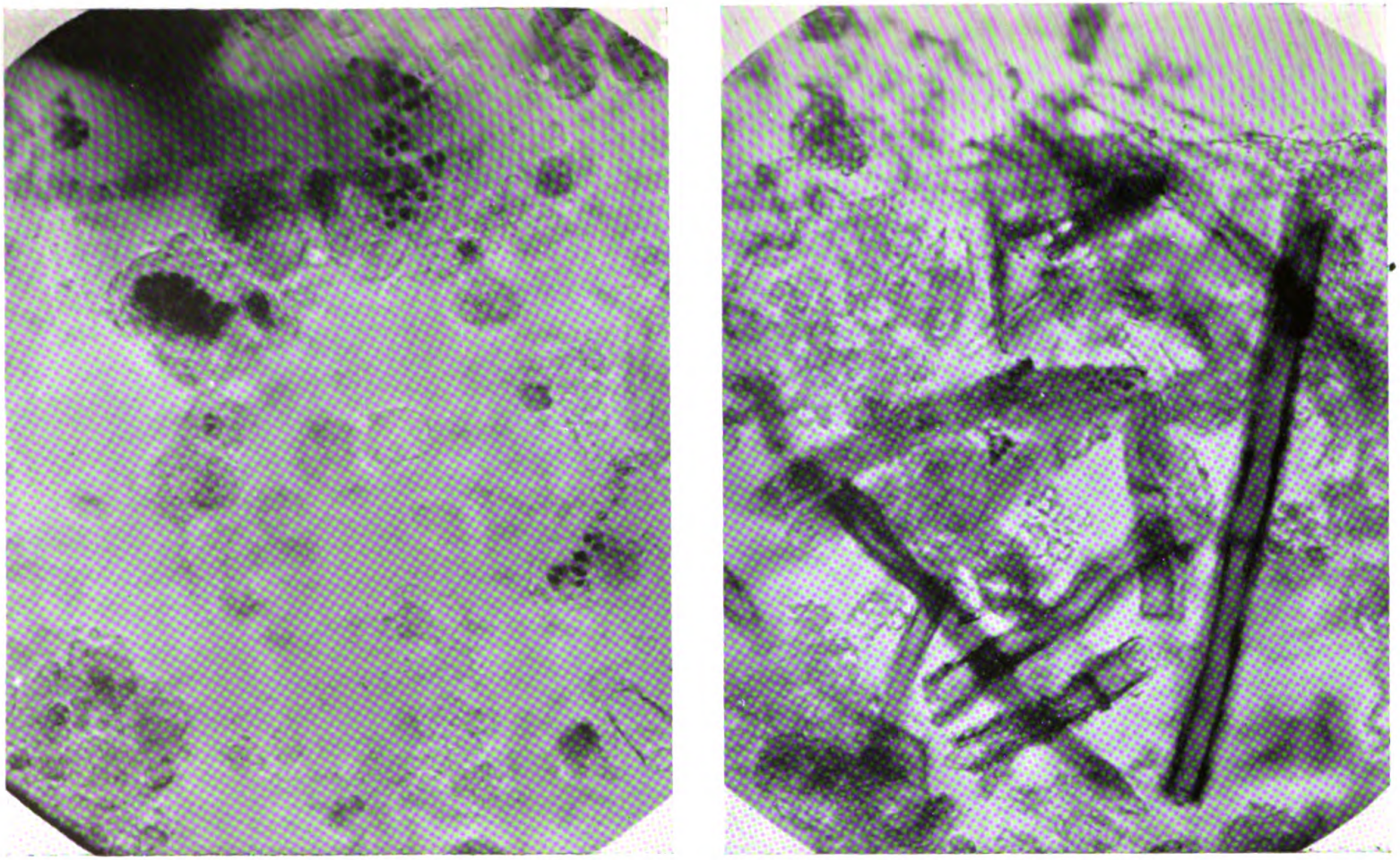
Related to base saturation are content of "available" lime and antacid buffering capacity, although the latter does not seem to be determined by the base content to the extent which might have been anticipated (Plice, 1934). In a material of very different types of humus layer, from the Adirondacks (Heimburger, 1934), the acid-soluble lime, expressed on a humus basis, ran remarkably closely parallel to the pH values. The rather scarce available data on antacid buffering hardly permit any definite conclusion to be drawn. One difficulty is the impossibility of correcting data obtained for equal weights of soil, to equal amounts of humus. Mull has been found to be remarkably low in antacid as well as in acid buffers (Hesselman, 1926); only in part could this be explained by a lower humus content.

As might be expected from the vegetation, there is a distinct difference between mull and mor with respect to nitrogen mobilization. Mull has practically always been found to be nitrifying, typical mor as a rule not nitrifying unless it is activated by some disturbance. This difference is seen also in material from this country (Romell and Heiberg, 1931; Heimburger, 1934). However, in the American material, nitrification was found to be not strictly confined to mull. Light forms of mor rather frequently nitrified. Even heavy mor, belonging to or approaching the greasy type, nitrified occasionally. These somewhat unexpected findings are paralleled by the unusual reactivity of the same American mor forms, as mentioned in the preceding section.

To summarize, a clear average difference in ecological environment has been found between mull and mor in two main respects. One is in acidity, and characteristics related to or governing acidity such as base saturation or content of available lime expressed on a humus basis. The other is in nitrogen mobilization.

The typical lack of nitrification in mor has frequently been explained by acidity and by scarcity of bases. In fact, the nitrifying organisms, even those thus far studied from forest soil, seem to be remarkably little tolerant against acidity (Winogradsky and Winogradsky, 1933). On the other hand, nitrification has been found to occur occasionally in forest humus of almost maximum acidity and poor in available lime (Romell and Heiberg, 1931; Heimburger, 1934). This may or may not be owing to the occurrence of centers less acid and higher in lime (Winogradsky and Winogradsky, 1933), as first suggested by Gaarder and Hagem.

Whether or not the differences in nitrogen mobilization are directly connected to those obtaining in acidity and related characteristics, both appear as fundamentally important. All the more puzzling is the fact that, as far as present knowledge goes, both are statistical differences only, and that it is not possible in either case to draw a clear dividing line even between pronounced forms of mull and of mor. The efforts made in Germany to separate "humus types" according to some sort of measured acidity do violence to nature, and can hardly be explained otherwise than as an expression of a curious modern tendency to regard everything recorded by apparatus in the laboratory as being more scientific than visual observations in nature.



A B

"HUMUS COLLOIDS" IN MULL AND IN MOR

A, Crumb mull (from Camillus, New York), ×1000, showing grape-like bacterial colonies with jelly capsules. Stain, rose bengal. Green light. Hom. imm., n. ap. 1.4

B, Greasy mor (hemlock mor from Heart's Content, Pennsylvania), ×1000, showing abundance of stumps of coarse, dark hyphae. No stain. Red light. Hom. imm., n. ap. 1.4

CURRENT IDEAS ON MULL AND MOR FORMATION AND MOR ACTIVATION

Following Ramann's lead, and more and more influenced by ideas of Glinka, Gedroiz, Ehrenberg, Wiegner, and others eminent in general soil science, forest-soil scientists have tended to abandon Müller's (1887) original biological concept of the primary differences between mull and mor. Gradually a common agreement has been reached on a body of doctrines of a more physico-chemical than biological pattern. According to this view, the differences in "microcosm" between mull and mor, strongly emphasized by Müller, are secondary. They are generally considered to be of importance only in so far as they influence the *rate* of decomposition of the litter material. Mull has come to be regarded as a result or a sign of rapid decomposition, mor as resulting from unfavorable conditions not permitting the decomposing organisms to do their work as rapidly and as completely as in mull (Romell, 1932).

Not only the soil life, but also the types of humus layer as such, have come to be looked upon as symptoms of the general conditions of soil formation rather than as being primarily important. Even most northern workers have identified mull soil with brown forest soil, forgetting the existence of the widely distributed mull podsol. The occurrence or non-occurrence of nitrification in the humus layer was referred by Hesselman (1917a) to assumed differences in the "electrolyte" supply from soil and ground-water, rather than to the directly observable differences between mull and mor. The characteristic structure of mull was interpreted largely in Ramann's way as a flocculation phenomenon due to the electrolytes held responsible for nitrification also.

The characteristic higher acidity and lower base content of mor, as compared with those of mull, are partly accounted for by assuming primary differences in base supply and by a varying acidity and base content of forest litter (Hesselman, 1926). What cannot be explained in this way is ascribed to differences in leaching or in rate of decomposition, or by an interplay of these factors. The ash constituents will naturally tend to accumulate in the humus formed during decomposition. This is counteracted by the leaching effect of rain and snow. With sufficiently slow decomposition, the latter effect will be the stronger one. This is taken to account for the formation of an acid mor from a less acid litter material, as when mor is formed under beech, a very common occurrence in Denmark.

Hesselman (1917 b) has used his "electrolyte" theory to explain also the effect of different forestry measures in activating a mor. For example, the effect of a clear cut was explained largely as a result of increased evaporation from the surface, with a resulting more upward trend in the wandering of the electrolytes. The good effect of green slash was in part referred to an assumed higher mineral-nutrient content in the green needles. The activating effect of a burn was taken to depend mainly on a concentration of bases in the remaining humus. As a partial explanation of the effect of disturbing the humus layer mechanically, an increased supply of mineral nutrients due to mixing with mineral soil was suggested first by Müller (1910). Hesselman (1917b) takes that as the main explanation.

The favorable soil effect of thinnings has been generally rather dimly explained by increased amounts of "light and air," or more specifically by a

more rapid decomposition due to increased soil temperature or moisture, or both; hence again a higher concentration of mineral nutrients in the humus.

The "electrolyte" theory thus applied locally as well as regionally has a great appeal by connecting the effects observed under one common point of view dominating also in general soil science. It is no wonder that the theory has been rather generally accepted, by foresters and by soil scientists.

Sporadic attacks only have been made against parts of the modern electrolyte theory. The most important of these attacks are believed to be the following. Müller (1924) pointed out that the existence of a widely distributed mull-podsol type presents a difficulty to acceptance of the theory. Hesselman (1926) found it impossible to account for the scarcity of antacid buffers in mull merely by a lower humus content. He hinted the importance of a different type of decomposition, as has been done recently also by several other northern authors (Gaarder and Hagem, 1921; Glømme, 1928; Brenner, 1930). The Jewish mycologist, Richard Falck (1923, 1926, 1928, 1930), has, even more specifically than the young P. E. Müller, referred the formation of humus with different acidity and different fertility level to the activity of definite organisms. A strong attack against the chemical conception of mull has unexpectedly come from Ramann's pupil and successor, Lang (1931). He gives reasons to show that the crumb-mull structure cannot be a result of flocculation by lime. He also has rediscovered several facts stressed by P. E. Müller and pointing to the importance of the soil fauna, particularly earthworms.

CRITICISM OF THE FOUNDATIONS OF THE CURRENT VIEWS

The foregoing rapid review of current ideas indicates that these are very largely based on the assumption of a consistent difference in rate of decomposition between mull and mor. It has been shown earlier (Romell, 1932), in some detail, that this assumption is not supported by facts and very likely does not correspond to the reality. Specifically, a comparison between two pairs of carefully selected localities in New York indicated that the total decomposition is slower in the best mull (crumb mull) than in a light mor (root mor), not faster as is currently taken for granted.

The following new arguments may be added. The current idea of a general slower decomposition in mor seems to be based simply on the fact that a greater number of yearly litter crops can be recognized in mor than in mull. The amount of decomposition may be very considerable, however, even though the plant remains are still recognizable as such (Ramann, 1911). When the litter is disintegrated and buried in the mull, this does not necessarily mean a greater loss of matter by decomposition.

In fact there are experimental results indicating not a more rapid decomposition, but a slower one, when the soil fauna is more efficiently engaged in the process (Falck, 1928; Ulrich, 1933). The total respiration of the soil fauna was found sometimes higher, sometimes lower, in beech mull than in beech mor (Bornebusch, 1930), with the mull averaging only 4 per cent higher; this in spite of the fact that probably more of the mor fauna than of the mull fauna was lost in sampling (Trägårdh and Forsslund, 1932). Since it cannot be denied that the mull fauna is more active than the mor fauna in making the plant remains unrecognizable, the result quoted seems to give additional evidence that the current conception about

the rates of decomposition in mull and in mor is simply the result of an optical illusion.

In reasonings on the current basis, it is at least very frequently understood that the humus accumulated is an undecomposed remainder of the original litter. It is further reasoned as if the humus colloids were much the same everywhere and differed in various types of humus layer essentially in base saturation.[5] Both views seem to be rather conclusively disproved by a direct microscopical study of the humus layer, using suitable staining methods. In the H-layer of very pronounced mor as well as of mull, the bulk of the humus appears to consist of living and dead organic material *built up* by the microflora active in decomposition. The microflora and the synthesized material are strikingly different when extreme types are compared, as in Plate I.

In the crumb mull (Plate I, A), jelly capsules of bacterial colonies apparently form a considerable part of what has earlier been regarded as "flocculated humus colloids." In the greasy mor (Plate I, B), fragments of brown, coarse hyphae are equally dominant. Remains of litter are rare, in the well-decomposed humus. It seems likely that the jelly capsules and the wall substance of the brown hyphae differ in chemical nature, not merely in base saturation. This points again to the importance of the type rather than of the rate of decomposition.

Strong objections can be raised against the current explanations of mor activation by forestry measures. A wandering of electrolytes upward from or through the podsol layer, sufficient to markedly influence acidity and base saturation of the mor and start a development towards a nitrifying humus layer, seems difficult to conceive in a humid climate, even on a clear-cut area. The good effect of green slash can hardly be due to a higher base content of the green needles, since the content of lime (the most important base) has been found to be lower and not higher in green needles and leaves than in ripe fall litter (Wolff, 1880). As to burning, the best effect is obtained by a very light burn, little more being done than to kill off the mor vegetation, and most of the increase in available lime content of the humus has been found to occur later and not as an immediate result of the burning (Eneroth, 1928). Neither of these findings would be expected from the electrolyte theory of activation. Finally, the activating effect of mechanical disturbances is by no means confined to cases in which the mor is actually mixed with or covered by mineral soil, as would be required by the electrolyte theory. Where actual soil-working has occurred, the reaction is frequently noticed on the mor around the worked spots rather than on the areas actually worked. This was pointed out specifically to the writer by the eminent Swedish forester, E. Ronge.

Decreased interception of light and rain is frequently taken as the cause of mor activation following thinnings. However, Danish foresters particularly experienced in thinning practices have pointed out that it is darker under stands properly managed by thinnings than under comparable unthinned stands. Yet it is in Denmark where thinning practices have shown the most remarkable effects on humus layer and forest production. Moreover, the general rule that the condition of the humus layer tends to

[5]This view has gained apparent support by recent findings (Mattson, 1932; Waksman and Iyer, 1932, 1933) on a "humus complex" or "humus nucleus" closely corresponding to the most important fraction of the humus which can be extracted with alkali from different kinds of natural humus or peat.

be better under well-closed stands (Hesselman, 1926) does not speak for a dominating rôle of the interception of sunshine and rain on the part of the stand. Finally, activation effects much like those produced by cuttings can be observed under undisturbed stands, as on trenched (Toumey, 1928), burnt (Gast, 1930), or raked (Fivaz, 1931) spots. A reaction similar to that following cuttings is indicated, for example, by the germination of seeds of Ribes (Fivaz, 1931) or of fire cherry (trenched plots at Dummer, New Hampshire, kindly demonstrated to the writer by Dr. Henry I. Baldwin).

FOUNDATIONS OF A BIOLOGICAL THEORY OF MULL AND MOR FORMATION

The current theories being unsatisfactory, it is time to look for new viewpoints. The studies of Müller and of Falck clearly indicate where to find building stones for a new theory. In fact, it is most curious that an evidently biological problem such as that of mull and mor formation has been commonly treated from chemical rather than from biological points of view.

In a pronounced mor, the soil life is completely dominated by fungi (Müller, 1887; Frank, 1888; Jensen, 1931). The fibrous type of mor is woven together by roots and by the hyphae of mycorrhizal and other fungi, so that the whole forms a tough felt or mat. This is not so much seen in greasy mor, but a microscopical examination shows the dominating rôle of fungi also in this type (Plate I, B). The mull harbors a relatively scarce fungous vegetation, and instead a more efficient animal life. This is evidenced by direct observation, by inference from the morphological characteristics of the mull, and by comparative analyses of the fauna in beech mull and beech mor (Bornebusch, 1930). In pronounced mull, bacteria appear very largely or almost entirely to take the place of fungi (Plate I, A).

The fungi and bacteria important in mor and in mull are, with few exceptions, unidentified, owing to shortcomings of the technic used in analyzing the soil microflora. Neither the visibly particularly important hymenomycetes nor the "autochthonous" (Winogradsky, 1925) bacteria develop in the petri dishes, with the methods used (Brierley, 1923; Falck, 1923; Waksman, 1930). Nevertheless, certain conclusions about the ecological importance of the different organisms seem to be permitted by the experience at hand.

Fungi attacking cellulose or lignin-cellulose often produce acid substances. Some of these may convert cellulose "quantitatively" to oxalic acid (Falck, 1930). Fungi of the brown-rot type, decomposing cellulose but not lignin, all seem to produce acidity (Falck, 1926, 1930), at least when growing on wood (Wehmer, 1925), because of the formation of free lignin if not of organic acids. Fungi of the white-rot type, decomposing lignin as well as cellulose, may (Glømme, 1928) or may not (Falck, 1926, 1930) produce acidity. Hyphae of some fungi have been found to give lignin reaction or to contain a soluble acid fraction resembling certain "humous" matter (Czapek, 1922; Rippel, 1931). Thus, when the bulk of the dead plant material is broken down by fungi, there are chances for a considerable production of acidity as a direct result of the decomposition or of the synthetic activity of the decomposing organisms.

Scattered observations with stored samples (Süchting, 1925; Hesselman,

1926; Glømme, 1932; Plice, 1934) indicate that a biological acidity formation actually occurs in mor. Several samples of very acid (greasy) mor changed their reaction to *less* acid in electrodialyzing experiments conducted in the writer's laboratory. This indicates that their natural acidity was due, not merely to extreme unsaturation of the humus colloids as a result of the leaching-out of bases, but also to actual production of acids.

The aerobic cellulose-decomposing bacteria, on the other hand, do not form acids (Waksman and Reusser, 1930), and the slime produced by some of the most important forms is so weakly acid that the reaction changed, in the cultures, in one or the other direction depending upon whether ammonium salts or nitrates were used as a source of nitrogen (Winogradsky, 1929). The jelly capsules of bacteria consist, so far as is known, of carbohydrates or sometimes proteins, not of distinctly acid colloids (Czapek, 1922). Anaerobic cellulose-decomposing bacteria producing organic acids may occur in crumb mull in the interior of the crumbs. Under the conditions obtaining, however, they would not be able to contribute much towards making the acidity higher, as is explained later.

With a bacterial type of microflora, as in mull, there seems to be only one chance left for any considerable biological production of acidity—namely, the liberation of lignin from lignin-cellulose. The bacterial decomposition of lignin has been little studied, but the microscopical picture offered by a crumb mull indicates a practically complete decomposition of the original plant residues in this most pronounced bacterial type. In an experiment with strawy manure (Falck, 1923), lignin was broken down as well as cellulose. This was a mixed type of decomposition much resembling natural mull formation, with bacteria and insect larvae acting together on the material. Also, the humus formed was neutral (later acid only because of an accumulation of nitric acid in the strongly nitrifying material). A beech mull was found to change its reaction to less acid as a result of decomposition of litter rich in nitrogen (Bornebusch, 1925), and this in spite of a strong formation of nitric acid. One-year-old beech litter was found to have changed its reaction to less acid in a mull locality, although the same kind of litter had changed its reaction to more acid in a mor locality (Bornebusch, 1930).

The facts discussed above indicate an important group difference between the bacterial mull type and the fungal mor type of decomposition. Not only is the mull equilibrium relatively neutrophilous, as compared with the acidophilous mor equilibrium; the former appears also as neutrogenous, the latter as acidogenous, as postulated by Brenner (1930). One reason for the mull being in biological equilibrium appears to be that acidity is not produced to any dangerous extent during decomposition. In mor, acidity is very likely produced as a direct result of decomposition, quite apart from leaching effects.

From this point of view, the more efficient animal life so characteristic of the mull must play a very important rôle in the maintenance of a mull equilibrium by keeping down acid-producing fungi. If the latter were left alone, they would easily start a progressive change towards more acid conditions, inimical to the mull life adapted to lower acidity, and a mor formation would be on the way. A mull condition thus maintained by the constant activity of animal guardians against biologically produced acidity must represent a rather delicate biological equilibrium. Anything weaken-

ing the soil fauna, even though it were only temporarily, might irreparably throw the equilibrium out of balance. A mor appears to represent an equilibrium incomparably stronger biologically, self-stabilizing to such a degree that a mor type would tend to become more and more pronounced once it had started to form.

The tendencies thus to be expected are in excellent agreement with a wealth of silvical experience. Danish foresters, and those of other countries, know all too well how easily a mor formation may be started as a result of some little carelessness, and what drastic means are usually required to revert the development so as to get back a good mull condition. An active formation of acidity by the humus life in the mor also makes it easier to understand how the mor can have such a striking and relatively rapid podsolizing effect on the underlying soil (Müller, 1887).

The rôle of the animal life in a mull equilibrium, and of the fungi in mor formation, was emphasized by Müller. More recently, Falck has claimed for fungus-devouring larvae and worms, and for certain fungi, a rôle still more specific than that suggested here. To Falck, mull formation always represents a white-rot type of decomposition interrupted by larvae and worms, and mor formation is ascribed to brown-rot fungi only, causing a progressive accumulation of acid humus from the undecomposed lignin of the litter. For several reasons, the writer prefers a less specific theory. The most pronounced mull does not have an F-layer, although it must have according to Falck's views. Even the heaviest (greasy) mor which the writer has examined seems to be built up chiefly by dead fragments of brown hyphae, and not by undecomposed lignin remains from the litter.

In the preceding reasoning, the difference between mull and mor in nitrogen régime has not been used and has not been accounted for. Nor has it been really accounted for by any previous theories, so far as the writer is aware. The difference, according to all indications, is not merely in presence or absence of nitrification, but in level of available nitrogen. The usual lack of nitrification in mor seems to be due less to acidity than to other factors. In Danish beech woods, Weis (1924) found the strongest nitrification in a district with very acid mull on acid soil. Mor samples among the most acid found may nitrify (Romell and Heiberg, 1931; Heimburger, 1934). The simplest explanation of the findings is that the occurrence of nitrification is governed principally by the level of available raw material (ammonia), as hinted in an earlier work (Gaarder and Hagem, 1921). In other words, nitrification would be a symptom of the level of available nitrogen more than anything else. This not only is in line with general microbiological experience, but also is indicated by the generally greater luxuriance on mull, both of forest growth and of ground vegetation.

The current ideas based on differences in rate of decomposition could not well account for the apparently better nitrogen supply in mull, even if the decomposition were actually consistently more rapid in this type. According to rules well established by microbiologists, excess nitrogen occurs in the form of ammonia or nitrates when the carbon–nitrogen ratio of the decomposing mass has decreased to a critical value, this differing somewhat according to the nature of the active organisms. This value may be higher or lower, and may take a shorter or a longer time to be reached, but it is reached sooner or later. Under balanced natural conditions, the only difference which would result from variations in rate of decomposition

would be in the number of yearly litter crops which would be furnishing available nitrogen. Their combined annual production of ammonia plus nitrates would be the same, if nitrogen fixation and denitrification are excluded. Nor would any difference be expected between mull and mor in level (concentration) of available nitrogen, since there is hardly any group difference as to the volume (depth) of the active strata.

The preceding reasoning applies, whether or not fungus-eating animals are engaged in the decomposition. For an isolated batch of decomposing material, an attack of larvae or of worms will thoroughly change conditions by rapidly mobilizing nitrogen stored up in hyphae, as in Falck's (1923) experiment. Under balanced natural conditions, however, this speeding-up of the nitrogen turn-over can be of no more importance than other variations in the decomposition rate. With the reservations made in the preceding paragraph, a constantly active mull fauna and flora could not be expected to furnish more available nitrogen yearly than would a soil life of any other type. The mull fauna cannot directly be a condition necessary for a satisfactory mobilization of the nitrogen contained in the litter, or even for nitrification. According to general microbiological rules, nitrification will set in as soon as excess nitrogen is mobilized as ammonia, provided only that the development of the nitrifying organisms is not inhibited by an excessive acidity or by any other factor.

The solution of the puzzle, according to the writer's views, lies in the structural differences between mull and mor. Characteristic of the latter is the abundance of fungus mycelia, many of which belong to the mycorrhizas of the trees and of the other higher vegetation. Practically everywhere in the whole mass of a mor, particularly in the fibrous types, there is a root, a mycorrhiza, or a hypha ready to absorb available nitrogen. The average distance between the points of production and of consumption of available nitrogen must be very short. In a typical mull, the roots are spread much like those of garden plants in a bed of good soil, and mycotrophy occurs to a much less extent. The path of diffusion of the available nitrogen to the absorbing organs must be considerably longer than in a mor. It follows that, *with the same turn-over* (production and consumption) of available nitrogen, the *nitrogen level* (average concentration) will be considerably higher in the mull.

The above reasoning is in line with ideas on the function of the mycorrhiza expressed by Stahl (1900) and utilized by later authors (Müller, 1903; Melin, 1925; Hesselman, 1926). It requires that the mycorrhiza hyphae shall be keen competitors for available nitrogen. This seems to be evident both from physiological (Melin, 1925) and from ecological (Hesselman, 1927; Melin, 1927) experiences, the latter having shown good mycorrhizas to develop only in humus samples where the nitrogen mobilization was good without mycorrhiza fungi. Such a result indicates that the mycorrhiza fungi are benefactors to their hosts, not by attacking ordinarily unavailable sources of nitrogen, but by serving as additional roots helping in the general keen competition for available nitrogen food.

With the viewpoint here proffered, the animal life of the mull actually has a rôle in creating a higher nitrogen level, but an indirect one. Its importance is to keep down the fungi which create by their omnipresence the low nitrogen level of the mor. The explanation allows the possibility of much the same nitrogen turn-over in mor and in mull. This seems to be an

advantage of the theory, since forest production has not been found consistently higher on mull.

Acidity and nitrogen level have been treated separately in the preceding reasoning. These factors must, however, influence each other in several ways. If organic acids are formed, their effect upon acidity, and hence upon leaching and base saturation, must depend very much on the nitrogen level. With a high nitrogen level, their effect must be nil or very low, since they are necessarily short-lived in the soil under such conditions, being excellent nutrients for a great many microorganisms. If available nitrogen is lacking, the organic acids can be utilized only by a few nitrogen-fixing organisms, and thus are likely to persist longer and exert a greater effect (Süchting, 1928). Their lifetime can be expected to be particularly long if the nitrogen level is low and at the same time acidity is high, since at least most nitrogen-fixing organisms seem to be little acid-tolerant. Relationships such as those pictured cannot be without importance for stabilizing a mor condition.

In the more acid mor forms, most or all of the nitrogen-fixing organisms are probably excluded. Under less acid conditions, nitrogen fixation is likely to occur. Nitrogen-fixing organisms have, in fact, been found in the better types of humus layer in the forest (Brenner, 1928), and fixation has been found to occur during the decomposition of leaf litter but only when the acidity was not too strong (Olsen, 1932). On the other hand, more nitrogen is likely to be lost as water-soluble humus from an acid mor poor in bases, than from a less acid type with more saturated humus. These losses may be considerable. If Aschan's (1932) figures are correct, Finland loses 1 kg of nitrogen per ha yearly in this way. This is probably about one-fourth of the combined nitrogen carried down by rain and snow. Finally, nitrogen may be stored away (in the form of a "humus nucleus" or otherwise) in the walls of the "almost indestructible" (Müller, 1887) brown hyphae forming a great part particularly of greasy mor, for so long a time that a régime is never reached and so this nitrogen has to be regarded as lost. All this makes it rather probable that not only the nitrogen level, but also the yearly supply of nitrogen, averages higher in mull than in mor, as is in fact indicated by the usually, although not always, higher productivity of mull soils.

The biological theory here outlined seems, better than do current conceptions, to account for the facts observed, and particularly also for the very puzzling diversity of conditions favoring mull or mor formation. The theory does not minimize the importance of either climate or lime content of the soil. It is evident that scarcity of lime and a very humid climate conducive to strong leaching must very generally favor acid-tolerant mor types of soil life, and make it more difficult for a mull type to establish and maintain itself. At the same time, the theory accounts, better than do current ideas, for a number of local variations and silvical experiences, such as the favorable effect of good, even, moisture conditions due to seepage water (even though very poor in lime) and of soil protection. The theory also makes it possible for one to understand why mull in poorer regions is frequently confined to moister situations, while in richer regions it occurs even on rather dry sites. Furthermore, the theory may settle controversies such as those between the young P. E. Müller on the one hand, and Ramann (1888) and Emeis (1893) on the other, with respect to the soil fauna as a

condition for mull formation. The bacterial mull equilibrium can evidently be maintained under good conditions, such as a sweet soil and a mild climate, with less activity on the part of the animal soil life than is required under less favorable soil and climatic conditions.

A BIOLOGICAL EXPLANATION OF THE ACTIVATION EFFECTS

It is shown in a preceding section that current ideas centering around the electrolyte theory must be very much strained to account for the striking effects on the humus layer abundantly observed as a result of various forestry measures. Biological explanations have been offered as supplementary, particularly for the effects of burning and of green-slash manuring (Hesselman, 1917 b; Eneroth, 1928; Juncker, 1930), but never as a common explanation of the activation phenomena. It has even been stated repeatedly that no biological explanation seemed possible (Hesselman, 1917 b: 975; Müller, 1924:79). In the writer's opinion, this is a fundamental misjudgment. A starting point for a biological theory is offered by the very remarkable high nitrogen mobilization in isolated lots of mor material.

Except for the most acid samples from the poorest types, the nitrogen mobilization in stored humus samples from mor has proved amazingly high, higher than in samples from better types of humus layer, including mull (Hesselman, 1926). This result is hard to reconcile with the ecological character of the corresponding types of humus layer. Hesselman (1926: 331, 528) suggests, as an explanation of the discrepancy, that nitrate nitrogen is a better nutrient than ammonia. This is not borne out by physiological data. The secondary unfavorable influence on certain crops, due to the acid ion of ammonium salts used as fertilizers (Kostytschew, 1926: 145), is an effect belonging entirely to the domain of agricultural chemistry. It cannot be of any importance in natural soils, where the ammonia is not added in the form of ammonium salts but is formed from proteins.

Hesselman also hints at the possibility of nitrogen less available being unintentionally determined as ammonia. This would be a very serious source of error, if nitrogen stored in living hyphae in the mor were included in the ammonia determination. Such does not seem to be the case, however, to any great extent, since the tests frequently have shown no ammonia present in fresh mor samples.

That the high nitrogen mobilization in most mor samples is real, is distinctly shown by culture experiments with mor material (Möller, 1902, 1903; Müller and Weis, 1906; Gyllenhammar, 1909; Holmgren, 1911) indicating a very good supply of available nitrogen in isolated lots of such material (not only when mixed with mineral soil, as the general result of these experiments has repeatedly been misquoted under the influence of the electrolyte theory).

The very high nitrogen mobilization in most mor humus isolated from its natural connection cannot well be explained simply by stopped root competition, since the values not only equal, but considerably exceed, those found with mull samples, even though the values are expressed on a humus basis. There must be a real increase in nitrogen mobilization as compared with the natural state.

In fact, stirring, mixing, and shaking has been found to enhance microbial activity, not only with various soils, but in general in disintegrated

solid material where microbial processes are going on (Petersen, 1871; Schloesing, 1897; Van Suchtelen, 1929). The effect has been explained as being due to improved aeration, but the fallacy of this explanation was clearly demonstrated by Schloesing (1897). He suggested instead that bacteria and unutilized deposits of food may be brought together as a result of the mechanical disturbance (Demolon and Barbier, 1931).

The general effect studied by Schloesing is not sufficient, however, to account for the higher nitrogen mobilization in mor samples, since mull samples would be likely to be affected in the same way. There must be some factor at work which affects the mor samples more than it does the mull samples. The structural differences between mull and mor point clearly to one such factor. It is simply the disruption of natural connections which inevitably accompanies the sampling of a mor. A mor has a definite and a more or less permanent architecture. Sampling a humus layer of this type necessarily means tearing off a great number of roots, and of mycorrhizal or other hyphae, which under natural conditions hold the mass together. Much of this material will be present in the sample in a state of necrobiosis. This sampling effect must be incomparably less pronounced with a typical mull, naturally worked by soil animals and consisting of crumbs or grains in loose layering.

The changes brought about by sampling a mor imply a radical alteration of the natural conditions of competition. In addition, the sample is fertilized with material formerly unavailable as microbial food because it was living; the sample is "green-manured." As a whole, the sampling effect could be compared to partial sterilization of soil (Waksman and Starkey, 1923), which has been shown to have a most striking effect in beech humus rich in fungi (Stahl, 1900).

The fungus flora of the mor is affected by the sampling in much the same way as when disturbed by soil animals. The microbial food made available is "green," relatively rich in nitrogen. When combined, this must strongly enhance microbial activity, and is also likely to change the soil life more or less in the direction towards a mull type. An abnormally strong nitrogen mobilization in the isolated sample can be expected, both from the increased activity, from the unusually high nitrogen content of the fresh raw material, and from the change to a more bacterial type of decomposition which is likely to occur (Waksman, 1930:45; Waksman and Starkey, 1931:94 ff.; Waksman, 1932:449–450, 744). This reasoning seems to give for the first time a reasonable explanation of the curiously strong nitrogen mobilization in stored mor humus. It has its principal interest, however, as applied to activation effects observed in forestry practice. Such an application is directly invited by the close correlation found (Hesselman, 1926, 1927) between nitrogen mobilization in stored humus, and the response of the corresponding mor to activating forestry measures.

The measures known to have an activating effect must, in fact, influence the life of the mor more or less in the same way as does sampling. This seems to be self-evident in the case of all kinds of soil-working. Burning and cuttings both have the effect of killing off great amounts of roots and their mycorrhizas. There must result both a green-manuring and a change in the competition conditions, such as is explained for the sampling. In the case of activation by green slash, the green-manuring effect is evident.

The slash cover also frequently kills off the mor vegetation more or less, resulting in an additional green-manuring and in freeing the mor from the strong grip of the mycorrhiza fungi belonging to the mor vegetation. (This is discussed further below.) The same points of view may in part be applied to liming practices. Curiously enough, a biological explanation of the activating effect has earlier been surmised in this very case, where, as an exception, the electrolyte theory appears satisfactory. Discussing some experiments with liming of heath soil, Müller (1913) suggested as a possibility that the principal rôle of the lime was to check the overwhelming competition from fungi (molds). Similar points of view on the effect of lime have been expressed more recently (Waksman, 1930:48). Lime differs, however, from other activating agents, except burning, by its favorable action being not only an indirect one. It also eliminates directly more or less of the acidity and low base saturation inimical to better types of humus life. This naturally explains its rapid and strong effect even though there may be little or no green-manuring.

The preceding reasoning seems to satisfactorily explain the curiously similar activation effects caused by very different measures and disturbances. The explanation offered is in line with the theory of mor formation given in a preceding section, but independently of this theory it suggests itself naturally from observational facts and experimental data. It is free from the highly hypothetical and partly improbable or even disproved assumptions upon which current explanations are based.

No more than current theories, can the present theory foretell the strength and duration of the activation effect. Thus it might be objected that, although a green-manuring and a weakening of the fungi must occur as a result of different activating measures, these effects may not explain the activation phenomena actually observed. New research, along lines indicated by the biological theory, is needed in order to answer any questions of a quantitative nature. It is known, however, that the addition of organic material is one of the most important factors influential in changing the microbial life of the soil (Waksman, 1930:45). The remarkable effect of immature plant material, in particular, is well known in agriculture. Green-manuring has been found, by stimulating the soil life, to mobilize nitrogen in amounts greater than are contained in the green-manuring material (Löhnis, 1926).

Green-manuring of a mor can be expected to be a particularly powerful factor, under favorable circumstances, for two reasons. Not only does it mean a quite exceptionally heavy manuring of the forest soil, but also it may induce a change in type of decomposition just as important as the pure fertilizing effect, or more so. As to the latter point, it seems obvious that one of the most radical means to secure a type change would be to let the humus formation start from the beginning on a sufficient amount of fresh raw material, under conditions favoring a better type of soil life in its competition with a present poorer type. Green-manuring not only furnishes the raw material, but also favors a better, more bacterial, more mull-like type of decomposition, as is explained in the discussion of the sampling effect. In addition, the green-manuring as effected by the different measures known to activate a mor, is almost invariably accompanied by influences directly weakening the fungus flora of the mor and thus further favoring a change in the direction towards mull.

It can be foreseen, from the standpoint of the theory, that different forms of mor will react differently, according to variations in structure, vegetation, acidity, and other factors. The greatest reactivity can be expected in humus layers of a decided mor character, but where acidity and other conditions do not too strongly predetermine a mor type of decomposition. Among the factors likely to interfere with the desirable reaction, one is a luxuriant mycotrophic ground vegetation. If this vegetation is not killed as a result of the activating measures, its mycorrhiza fungi may offset the activating effect by maintaining a low nitrogen level, and a normal mor condition may soon again be stabilized.

The rôle, in mor formation, of dwarf shrubs such as blueberry bushes and heather, has been the subject of much controversy. Practical foresters, basing their judgment on observation and experience, have extensively regarded those plants, which are characteristic of many forms of mor, as harmful forest weeds directly contributing to mor formation. The opinion of scientists has been and still is divided. Recently, under the influence of the electrolyte theory, there seems to be an increasing tendency, even among foresters, to look upon the dwarf shrubs, like the other mor vegetation, as purely secondary, merely indicating a mor condition. Yet some foresters maintain the old view in opposition to scientific authorities (Hassenkamp, 1928).

The present biological theory supports the old interpretation of the blueberry bushes (Müller, 1887:161, 1924:168) and other dwarf shrubs as actively important in creating or maintaining a mor condition. In doing so, the theory seems to account for some puzzling facts. One of these is the opposite effect of clear-cutting in northern Sweden and in the Black Forest in Germany, mentioned in a preceding section. This difference is paralleled by an opposite behavior of the blueberry bushes (Hesselman, 1926: 361). In north Sweden, these degenerate and gradually disappear when fully exposed; in the Black Forest, they luxuriate on clear-cut areas. The modernists taking this difference as a secondary effect must explain the progressive mor formation on clear-cut areas in the Black Forest by poorer conditions for decomposition there than in Lapland. This is an utterly improbable assumption. It is more likely that the activation effect is offset and reversed by the mycorrhizas of the luxuriating blueberry bushes which the summer droughts in the Black Forest are not sufficient to kill, even on clear-cut areas.

The unfavorable effect of selective diameter cutting in north-Swedish spruce forests is also accompanied by a greater luxuriance of the blueberry vegetation in treated than in untreated stands. This fact may again very well be the primary one. Apparently the sunshine is not strong enough in the selectively cut stands to kill the blueberry bushes, although it does kill them on clear-cut areas in the same region.

In fact, many observations by foresters indicate a very direct harmful influence of the dwarf shrubs accompanying poor forms of mor. One of the most striking and best-studied instances is the relation between heather and spruce in the heaths of western Jutland. As soon as the heather closes over the ground around the young spruce, a characteristic stagnation of the latter, with chlorosis of the needles, very regularly sets in. This can be remedied by renewed soil-working, but is likely to repeat itself at any time until the plantation is closed and the heather is definitely crowded out.

The exact reason for the heather injury has been a mystery: "Here we stand before an x, an unknown factor; it would be of the greatest importance to find out whether it is physical or chemical in nature or belongs to the domain of soil physiology" (Müller, 1897).[6] The modern tendency, most pronounced with Süchting, has been to solve the mystery by denying the effect, taking the heather as a simple indicator of poor conditions. This does not do justice to a wealth of experience from western Jutland, nor, in particular, to the very interesting exceptions from the general course of events. One of those exceptions is that the stagnation is not noticed on heath land previously farmed, even though the heather may close completely over the ground (Müller, 1897).

From the standpoint of the biological theory, largely developed earlier by Müller (1903, 1910, 1913) in this particular case, both the generally observed heather effect and the mentioned exception to the rule seem easy enough to understand in principle, as follows. The heather, through its mycorrhizas, lays a dead hand over the humus formation, which suffers also from lack of raw material since the young spruces shed very few needles. The plantation suffers if the new humus formation dominated by the heather is the only nitrogen source. Yet, if there is an old culture horizon, this may harbor for a while a more favorable humus life furnishing the necessary nitrogen to the young trees. The well-known favorable influence exerted by pines (Müller, 1903) may be due simply to their furnishing more raw material for the new humus formation.

The following observation, made by the writer when visiting one of the late Dr. F. Weis' experimental plantations on heath land in western Jutland, apparently illustrates how radically conditions are changed by simply killing the heather, without any soil-working. Outside the plantation, some straw used as packing material had been left in a pile on the raw heath. The straw had settled considerably and had taken a grayish color, but it appeared very little decomposed. Yet it had been there long enough to kill the natural heather vegetation which it covered. A strong reaction was the result, as was evidenced by tall, luxuriant, flowering specimens of a nitrate plant, *Chamaenerion angustifolium*, breaking through the straw cover.

The abundance and vitality of dwarf shrubs is very likely a factor of general importance in influencing the reactivity of different forms of mor. The commoner occurrence of Vaccinia or Calluna in the flora of most of the heavy forms of European mor may be a clue to the understanding of their much lower reactivity as compared with American mor forms of a more or less greasy type, even extremely heavy and acid ones. The more herbaceous vegetation of the latter, with Vaccinia and similar dwarf shrubs missing or playing a subordinate rôle, cannot dominate the mor by its mycorrhiza hyphae to nearly the same extent as does a blueberry or a heather vegetation. Thus the felling of a tree means a relatively more extensive weakening of the symbiotic fungi in the surrounding mor. An activation effect due to green-manuring will be easier to start and will not so easily be offset by remaining mycorrhiza fungi as in most European forms of heavy mor.

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[6] Translation from the original.

SILVICAL APPLICATIONS OF THE BIOLOGICAL THEORY

The theory which the present paper contributes, like the older ones which it supplements, will be useful in correlating silvical experiences and in guiding silvical thought rather than by furnishing directly new practical recipes. It suggests, however, experimentation along partly new lines, and, if further corroborated by experience, it should influence forestry practices to some extent. Significant new experimental evidence can best be obtained in the forest. The effect of killing a luxuriant mor vegetation should be studied. New methods of soil preparation, effecting a trenching rather than a soil-working in the ordinary sense, should be tried for experimental purposes.

In judging the experimental results, it will in most cases be difficult to distinguish between the effects discussed in this paper and the effect of lessened root competition in the ordinary sense of that expression. From a practical point of view, this is of little importance in experimenting with different activation measures. In other practices the case may be different, as in judging the most favorable space of planting under different conditions. If root competition between the trees themselves is the more important factor, a wide spacing would be generally indicated on dry and poor soil, as actually recommended by Süchting (1929 a, 1931). If the influence of the symbiotic fungi in one direction, and of green-manuring in the other, is particularly important, as suggested by the biological theory, close planting would be indicated in many cases, even on poor soil, in order to get quickly a closed stand and crowd out a harmful ground vegetation. Close planting followed by frequent thinnings would, in general, be expected to yield a better result than would wide spacing from the beginning. Contrary to current ideas on root competition, the new theory distinctly militates against the very wide spacing in forest planting recently advocated in this country. Only in certain cases—as, for example, if the site is very dry and poor and yet does not tend to be invaded by a harmful ground vegetation—can a wide spacing be expected to be better.

Probably the principal practical use of the biological theory, if it proves to be sound, will be in helping to find new, cheaper, or better methods of soil preparation for use in forestry practice. If the most important effect of soil-working and burning is to kill off the mor vegetation, these measures may advantageously be replaced by cheaper or less hazardous methods, as, for example, by some spraying technic.

One achievement of the theory is to explain the remarkable soil effect of the modern frequent and strong Danish thinnings, as practiced particularly on Frijsenborg by E. Moldenhawer. The amazing results obtained, with primary conditions of soil and climate not particularly favorable, are a challenge to the forestry profession in general. From the standpoint of the biological theory, it can be hoped that the Danish experiences will have a rather general application in principle, if the thinnings are supplemented, where needed, by some suitable treatment controlling a harmful ground vegetation. Thus the theory encourages foresters in other countries to try to meet the Danish challenge, and it may help them to attain similar apparent site-improvement effects and remarkable yields where conditions permit the use of intensive methods.

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